

# Field Observations on the Flexibility of the Acoustic Behaviour of the European Bat *Nyctalus noctula* (Schreber, 1774)

by

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With 4 figures

## ABSTRACT

The amount of variability in the sonar emissions of free flying European bats is scarcely known. This paper describes how the structure of the echolocation signals of *Nyctalus noctula* (Schreber, 1774) correlates to the height of flight, and to the varying density of obstacles in the flight path.

Search pulses of bats flying close to the ground or near obstacles were short and of high frequency and large bandwidth. So far, these signals were not known to be typical for noctules. When the bats moved close to the ground in open areas, a succession of pulses suited to prey detection and of pulses suited to general orientation was found. The observed pulse structures are discussed with regard to their function in the acoustic orientation of the bat.

A precision broadband ultrasound detector, developed by the author, was used to convert the signals to the audio range. A block diagram of the device is shown.

## INTRODUCTION

Only little is known about the extent to which free flying European bats vary the properties of their sonar signals. The difficulties of observing bats in the field under carefully controlled conditions may be one important reason for this lack of data. The

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observation of the acoustic behaviour was impeded further by heavy and bulky acoustic equipment that could not easily be transported to interesting localities.

In recent years, lightweight electronic detectors have vastly improved this situation. At present, new detectors with a higher performance, and digital memories with the ability to slow down signal sequences of several seconds duration, are made available. These instruments will allow to overcome some of the difficulties mentioned above.

The present paper aims to demonstrate a possible application of the new detector technology to the study of bat echolocation behaviour. An assessment of the variability of search calls emitted by free flying *Nyctalus noctula* was made.

Some general information on the structure of echolocation signals of *Nyctalus noctula* in free outdoors flight was provided by HARTLEY (1985), MILLER and DEGN (1981), VOGLER and NEUWEILER (1983), PYE (1980) and AHLEN (1981).

The greater noctule (*Nyctalus noctula*) is known to hunt in open space, usually at tree level or above. Occasionally, however, *Nyctalus noctula* can be observed to move down and hunt close to the ground level, sometimes even among trees.

The sonar theory suggests that the signal type emitted by a bat for its general orientation or for prey detection, should not be the same in an obstructed environment and in open space.

In any natural habitat it is difficult to assess quantitatively the degree of obstruction in space. Therefore the simplified hypothesis was set up by the author, that the signal structure should generally be influenced by the flight level above ground. Different flight levels do of course include a change in the degree of obstruction.

When the bats would change from a high to a low flight level, I expected to see a change from long range search calls of long duration, low frequency and with a shallow frequency modulation, to shorter search calls with a steeper modulation and of higher frequency.

At a high flight level, noctules usually emit search pulse sequences which sound like 'blop-blop, blop-blop', when they are made audible by means of a broadband detector (see also MILLER and DEGN, 1981). These are sequences of pulses alternating in their structure. The 'blips' are of higher frequency and of higher bandwidth than the narrowband 'blops' and are usually followed by a longer pulse interval than the 'blops'. Since this type of signal is only common for noctules flying at high level, some insight in the function of this particular signal property should also result from testing the above hypothesis.

## METHODS

The signals were picked up by a QMC microphone and then fed to a precision divider circuit (Type V1.3, developed by the author \*) which reduces the signal frequency by a factor of eight, but preserves the original signal duration, envelope and modulation. A block diagram of the device is shown in Fig. 1. This type of instrument cannot cope properly with a complex harmonic signal structure. If several strong harmonics are present, the device follows the harmonic with the highest amplitude in each case. Distortions of the signal envelope produced by the superposition of several strong harmonics are however preserved by the detector.

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\* More information about the detector, which is commercially available, can be obtained from the author.

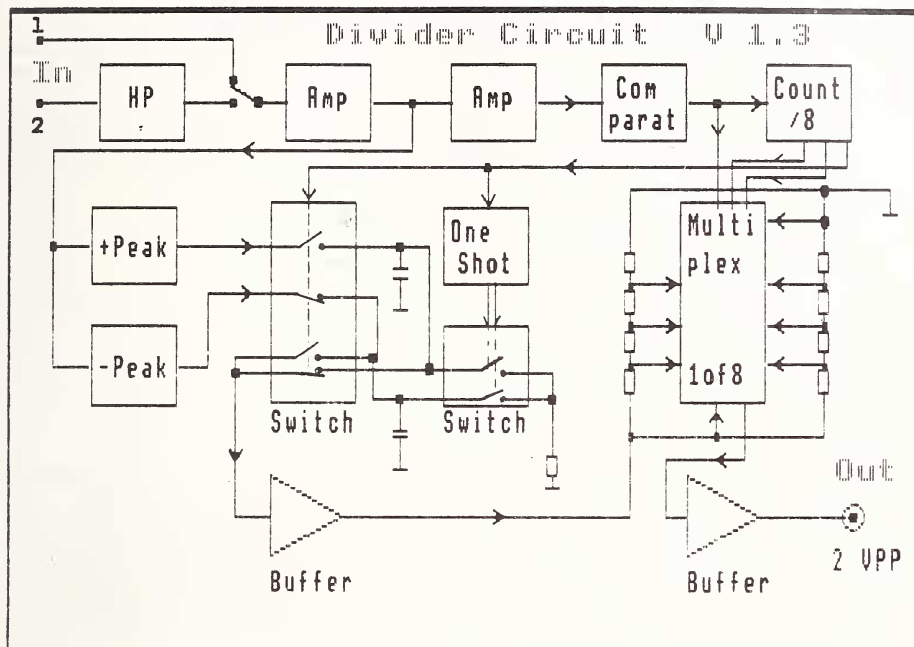


FIG. 1.

Block diagram of the broadband ultrasound detector V 1.3. The instrument is driven by an external ultrasound microphone and preamplifier stage. A 20 kHz HP-filter can be switched into circuit (Input 2) in order to attenuate audio noises. Signal frequencies in the range of 10-220 kHz are converted to 1.25-27.5 kHz by means of a counter circuit which controls the switching of a multiplexer. The input voltages to the mux are set up by a resistor ladder, which is designed to produce a step by step approximation of a sinusoidal waveform at the output of the circuit. The voltage which drives the resistor ladder at any one moment is derived from the positive and the negative signal envelope, sampled over eight signal periods by the peak detectors and switches. The original signal envelope is very faithfully reproduced at the output since the system has an excellent overall linearity. The wideband S/N-ratio over the full frequency range is about 55 dB.

The detector output was recorded on a Sony TC-D5 high quality, portable cassette recorder. The detector + recorder system had an overall frequency response of 10 to 130 kHz ( $\pm 3$  dB). The upper limit was given by the tape recorder.

The recorded signals were subsequently analysed with a period meter (developed by D. HARTLEY and the author) and a digital oscilloscope (Nicolet, type 3091). The instantaneous signal frequency could be measured to a resolution of 0.8 kHz by means of this equipment.

Recordings of many different individuals of *Nyctalus noctula* were made at a number of localities in the central and western parts of Switzerland in 1985-86.

The flight behaviour of the bats was observed and a commentary was recorded on a second track on tape. Under field conditions it is not very easy to judge the height of bat flight above ground. To make the judgement sufficiently reliable, only two categories

of flight behaviour were distinguished at the time of data evaluation: search flight above 15 m and search flight below 15 m. This level was arbitrarily chosen as a reference. It had the advantage of being easily recognised since it approximately corresponded to tree level at most observation sites.

Target approach sequences with or without terminal buzzes were not looked at. For the analysis, the recordings of all the localities were pooled and the samples to be analysed were randomly selected.

The following signal characteristics were checked:

- the intervals between search pulses
- the pulse duration
- the instantaneous frequency at the pulse centre (e.g. at half duration) and
- the end frequency of the sweep.

## RESULTS

Figure 2 shows a sample of about 240 intervals between search pulses for each flight level. At both flight levels the distributions appear to be multimodal. The different modes do most probably correlate with the average wing beat rate of the bats and with its multiples as has been suggested by HARTLEY (1985) for noctule search flight in England. At high flight levels, longer intervals were more common with a highest mode at 275 ms. At low flight level, the highest mode was at half that value with 130 ms. No systematically occurring change in flight speed of bats flying high or low could be observed.

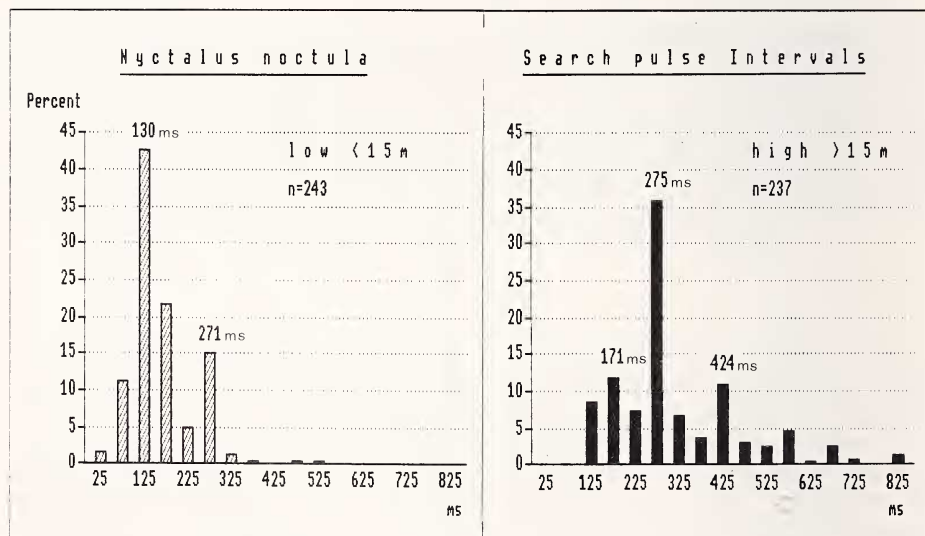


FIG. 2.

Intervals between search pulses emitted by bats flying at low level (< 15 m) and at high level (> 15 m). The histograms show a multimodal distribution in both cases. The class width is 50 ms. The numbers above the peaks are the values in ms of mode 1 and 2 (low) and mode 1, 2 and 3 (high).

Thus the data suggest that at high flight level the emission of one search pulse per every two wingbeats is most common. One pulse per wingbeat or one pulse per four wingbeats also occur, but less frequently. The data would indicate an average wingbeat rate of 6 per second. At low level, on the contrary, one pulse per wingbeat seems to be the rule. No distinction between 'blips' and 'blops' was made at this stage.

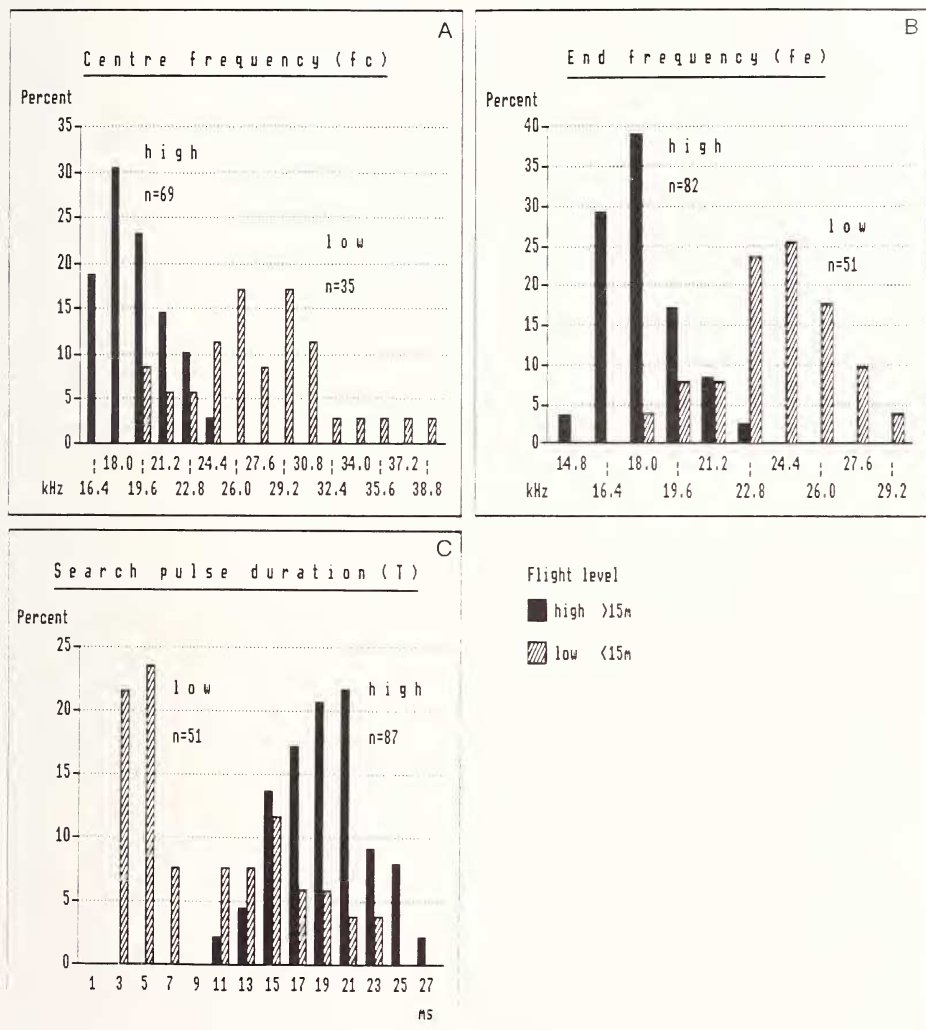


FIG. 3.

Histogram plot of three important search pulse parameters. Two pulse samples were taken from bats flying at low (hatched bars) and at high level (solid bars). The values in A and B were obtained from a random subset of the total number of pulses used for C.

A: Instantaneous centre frequency (fc), class width 1.6 kHz.  
 B: Instantaneous end frequency (fe), class width 1.6 kHz.

C: Pulse duration (T), class width 2 ms.



In Figure 3c the total pulse durations of two signal samples taken at high and low flight level are shown in histogram form. At high levels the mode of the pulse duration was at 20.2 ms and the distribution was more or less unimodal. At low flight levels, the distribution appears to be bimodal. The first, higher mode at 4.2 ms results from signals emitted by bats flying very close to the ground, that is, only 1.5-3 m above it. At higher levels, but still below 15 m, the signals were longer, but with an average of 15 ms still not as long as at flight levels above 15 m.

The centre frequency (Fig. 3a) was widely dispersed at low flight levels. This points to a high variability in the modulation rate and consequently in the bandwidth of these shorter signals.

At high flight level, the distribution was much more uniform and had a median value of less than 19 kHz as opposed to 27 kHz in low level flight.

The end frequency, whose distribution is shown in Fig. 3b, is the one parameter which is most distinct in the two situations. At high level, the end frequencies of the shallow frequency modulated pulses had their median at 17.9 kHz. Some signals extended down to 15 kHz in high altitude search flight. At low flight level, the end frequencies varied between 18 and 29 kHz with a median of 24.0 kHz.

All the data we have looked at so far support the hypothesis that the flight level of a noctule has a strong influence on the design of the search signals. But we still can not decide to which extent this influence is due to the distance from the ground itself or due to the change of the density of obstacles in the flight path of the bat, which changes with the flight level. This point is now discussed in more detail by means of two further observations:

1.— On several occasions, recordings were made from bats hunting at low level (below 10 m) over open land and water near Berne. In this situation the bats had almost no obstacles in their way. They emitted search calls which were of long duration and of a low frequency, narrowband nature. The bats also produced the 'blop-blop'-pattern which is typical for noctules search flight at high level. The 'blops' were generally of lower frequency and higher intensity than the consecutive 'blips', and the pulse intervals were usually longer after 'blips' than after 'blops', just as in the case of a high flight level. The 'blops' were very similar to those emitted at higher levels. Figure 4a shows an oscilloscope trace of a typical 'blop', emitted at low flight level, together with its period plot. It had a duration of 22 ms, a total sweep-bandwidth of about 1.5 kHz and an end frequency of 18.4 kHz. The rapid onset is typical for 'blops' and indicates a formant at the start frequency of the pulse.

The 'blips', however, ended at a comparatively higher frequency, and their modulation rate was steeper than in ordinary high level search flight. A 'blop' emitted at low flight level over a flat area is shown in Fig. 4b. It had a duration of 17 ms, a total sweep-bandwidth of 16 kHz and an end frequency of 22.4 kHz.

2.— In 1985 I recorded a single noctule which was hunting at a very low level, that is 1.5-3 m above ground among the stems of nut and cherry trees at Onnens (Canton VD). It did this for a few minutes and then went up to fly above the trees for a short while, only to come back down again and repeat the sequence. This happened several times. The situation was very interesting because it excluded any possibility of interindividual variability. At high level flight, the ordinary 'blop-blop'-sequence could be heard, which allowed the identification of the bat in the first place. Figure 4c shows a typical signal. With a total duration of 16 ms, a sweep bandwidth of 1.6 kHz and an end frequency of 17.6 kHz the 'blop'-type pulse fits well in with the high level pulse population we have characterized before.

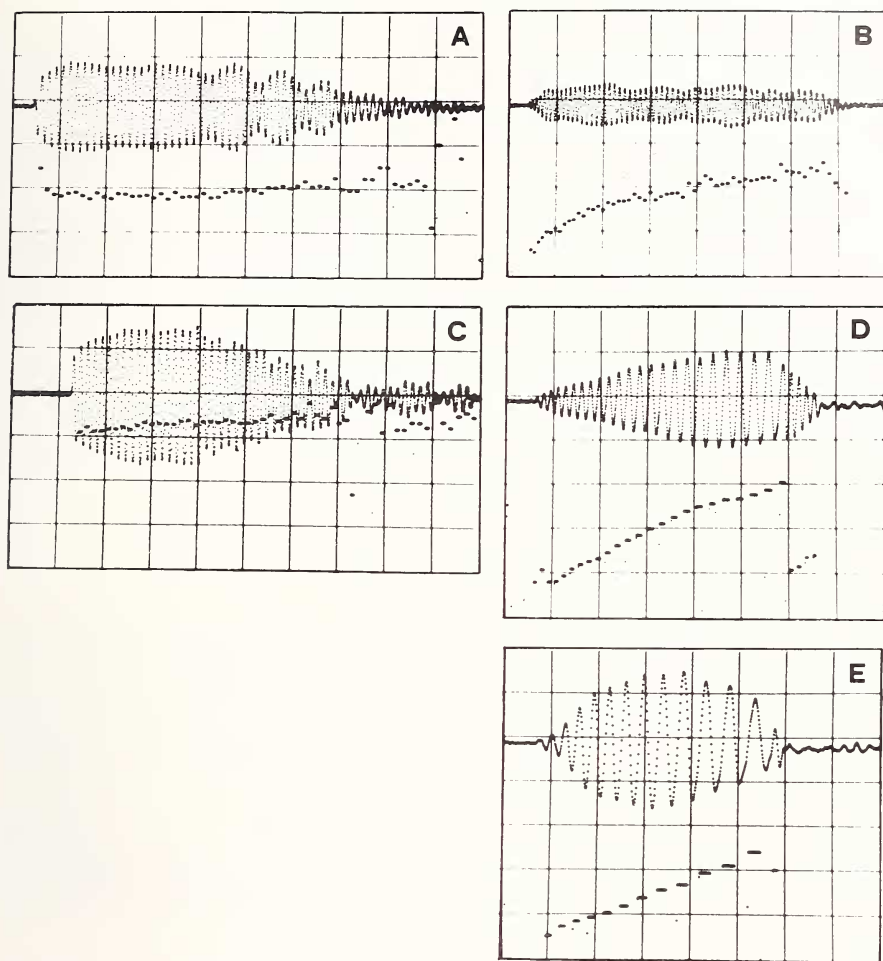


FIG. 4.

Typical search signals recorded from bats flying at various levels above ground. The recordings were obtained by means of a broadband detector (V 1.3). The upper oscilloscope trace shows the waveform and the lower trace shows the period plot in each case. See text for a more detailed signal description. 'Blop' (A) and 'Blip' (B) were emitted at a flight level of approx. 10 m in open space. Horizontal axis 2.7 ms/div.

C-E show search pulses emitted by the same bat at various levels above ground. C: 'Blop' emitted at high level flight above the trees (> 15 m). Horizontal axis 2.7 ms/div. D: Search/orientation pulse emitted at a flight level of 3 m above ground. Horizontal axis 1 ms/div. E: Search/orientation pulse emitted at 1.5 m above ground when the bat was moving at high speed among the stems of the trees in an orchard. Horizontal axis 0.5 ms/div.

When the bat moved to a lower level, the signals became gradually shorter and higher in frequency and bandwidth. This is shown in Fig. 4d which represents a signal sample, recorded when the bat was flying at about 3 m only. The pulse shown was 6 ms long. The presence of a strong second harmonic is indicated by the asymmetry of the envelope towards the end of the signal and by the discontinuity which is visible in the period plot and in the waveform. The bandwidth of the fundamental was then already 30 kHz and the end frequency had gone up to 24 kHz.

When the bat moved again closer to the ground and flew between the stems of the trees, all the pulses became very short indeed, and their sound pressure level dropped markedly. Most of these pulses were of linear period modulation and were only 2-3 ms long. The sample shown in Fig. 4e had a sweep-bandwidth of more than 33 kHz and ended at almost 29 kHz.

The bats always maintained the pulse intervals long enough to avoid an overlap of the outgoing pulse with the ground echoes of the previous pulse. The bats accomplished this by keeping the search pulse intervals longer than 100 ms at high level flight (> 15 m). This held true even for the shorter intervals after 'blops', thus assuring that there was no overlap between the ground echoes of a 'blop' and the following 'blip'.

## CONCLUSION

To conclude we can say that both, the distance to the ground and the density of obstacles have an influence on the structure of search calls in *Nyctalus noctula*.

The calls are of long duration, small bandwidth and low frequency, when the bats fly high and in open space. The bandwidth and the end frequency of the 'blips' is then only moderately higher than of the 'blops'. These are typical characteristics of signals which are optimised for long range target detection and for long range orientation.

At a lower flight level, the influence of obstacles does not allow for such long detection signals unless the flight path is essentially free of any obstacles. In such a case, a high sensitivity for long range detection is realised by means of signals which are similar to the high level 'blops'. The 'blips', which were shown to have an increased frequency and bandwidth compared to 'blops' emitted at high flight level, provide the necessary accuracy in ranging when the bats are flying low.

Whenever the bat is manoeuvring very close to the ground at high speed, however, it requires accurate short range information and a high information density in time. This calls for short, wideband signals, emitted at a high pulse rate. The signal type described above fits well in with these theoretical estimates. The higher harmonic present in these signals does increase the overall bandwidth and helps to further improve the range resolution (ZBINDEN, 1988).

This investigation suggests that the individual variability in the search call structure of *Nyctalus noctula* is rather higher than has been anticipated in the past. The information presented in this article may therefore be of interest to anyone who applies bioacoustic methods to species identification and census work in the field.

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